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Diet and Feeding Habits of *Octopus hubbsorum* Berry, 1953, in the Central Mexican Pacific

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Abstract. The diet and feeding habits of *Octopus hubbsorum* were analyzed using 226 individuals obtained from commercial artisan catches in the Central Mexican Pacific from July, 1999, to August, 2000. Organisms ranged from 43 mm to 230 mm in dorsal mantle length. The diet comprised 53 types in seven phyla; crustaceans, mollusks, and fishes were the main groups. In general, the crustaceans were dominant; in particular, species of brachyurans, carideans, and anomurans, with values of more than 40%, according to the index of occurrence and the indices of importance in weight and number. The diet is affected by sex, size, sexual maturity, and the season of the year. The females fed preferably on mollusks (gastropods and bivalves) and had a higher proportion of food in their stomachs than males, while the males fed mostly on crustaceans and members of the group "others." The type of prey and its proportion also vary as the organism grows; the juveniles contained a lower number of prey species than the mature individuals. The males showed a clear tendency to increase the number of prey groups from warm to temperate environmental conditions. These results confirm that *O. hubbsorum* is an opportunistic predator.

INTRODUCTION

Octopus hubbsorum has a wide geographical distribution, ranging from the central Gulf of California (28°55′N, 113°32′W) to the southern coast of Oaxaca, Mexico (16°10′N, 95°14′W) (López-Uriarte et al., 2005). It constitutes practically half of the catch of the octopus fishery in the Mexican Pacific, totaling nearly 1000 tons per year (SAGARPA, 2002). During the last decade, this resource has occupied one of the first five places of the coastal fisheries of Jalisco (Ríos-Jara et al., 2004).

Octopuses are ferocious carnivores, feeding during the day or night on a wide variety of prey species, which are detected either by vision or by touch (Hanlon & Messenger, 1996). At all stages of development, octopuses are active predators, feeding mainly on crustaceans, mollusks, and fishes; but ophiuroids, polychaetes, chaetognaths, and siphonophores constitute part of the diet of some species. The proportion of these types of food depends on the species, the sex, and the sexual maturity of the individuals (Nixon, 1987). Because of their opportunistic behavior, prey density also has an important effect on feeding; the octopods consume the most common prey available in their habitats (Wolterding, 1971; Hochberg & Couch, 1971; Hanlon, 1975; Van Heukelem, 1976; Ambrose & Nelson, 1983; Ambrose, 1984). However, mature females reduce their intake of food by up to 50% two weeks before spawning and for at least three weeks afterward; feeding is also reduced during the winter when temperatures are under 15°C (Borer, 1971).

There have been no studies on the feeding behavior and diet of *O. hubbsorum*. The only previous report was made from observations of the shells of gastropods and bivalves found outside the caves and shelters of adult octopuses living in the shallow rocky areas of Bahia de Coastecomate, Mexico (19°13′47″N and 104°43′44″W) (Raymundo, 1995).

The present study aims to describe, first, the diet of *O. hubbsorum* in the central Mexican Pacific through the analysis of stomach contents, and, second, the feeding dynamics using different indices to evaluate the possible effect of sex, size, stage of maturity, and the seasons of the year. This contribution to the studies of the Mexican species of octopuses is the first detailed description of the feeding habits of this species.

Figure 1.

MATERIALS AND METHODS

Area of study: The littoral of Jalisco is located in the central Mexican Pacific (between 20°40′N and 18°58′N). This study was conducted in the central region of Jalisco, where *Octopus hubbsorum* is exploited commercially. This region extends approximately 38 km from Punta Soledad (19°36′47″N, 105°12′13″W) to Punta Farallón (19°23′22″N, 105°02′17″W) (Figure 1). The coastline of this region is characterized by sandy beaches alternating with rocky shores and cliffs. In the shallow areas, there is a complex substratum of bedrock, boulders, rock rubble, and sandy bottoms, with small rocks interspersed with patches of sand covered with a layer of fine sediment consisting largely of detritus particles. The more heterogeneous rocky bottoms have higher abundance and a greater variety of macroalgae, invertebrates, and fishes. In some of these areas, several species of stony corals (*Pocillopora* spp. and *Porites* spp.) grow together, forming aggregations with a characteristic flora (macroalgae) and fauna (crustaceans, echinoderms, molluscs, polychaetes, gorgonians, and fishes).

The region has warm–wet climate, with the rainy season occurring mostly during the summer. Temperatures range from 32.3°C in September to 20.6°C in January (mean = 25.2°C) (Secretaría de Programación y Presupuesto, 1981). The surface-water temperature of Bahia Chamela is higher from June to September (26.0–30.6°C) and lower from February to May (22.8–26.6°C); the difference between the maximum value (July = 30.6°C) and the minimum value (February = 22.8°C) is approximately 8°C (Silva-Segundo et al., 2006). Cumulative monthly precipitation ranges between 800 mm and 1500 mm, with the highest values from June to September and the lowest from February to April (Villalpando & García, 1993). There is a mixed semidiurnal tidal cycle with two unequal high tides and two unequal low tides each day. The region is strongly influenced by tropical storms and cyclones during the warm-wet season. Coastal waters are relatively productive and have the influence of three main surface currents: (1) the North Equatorial Countercurrent, with warm waters from the south (June–September); and (2) the Gulf of California Current (October–January) and (3) the California Current (February–May), both of which bring cooler waters from the north (Wyrtki, 1965, 1966). Therefore, there is well defined seasonality with three main seasons during the year: (1) a warm–wet season from June to September, which corresponds to the rainy period of the year, with warm surface-water temperatures higher than 26°C; (2) a warm–dry season from October to January, when the surface-water temperature is still warm and the rainfall is scarce or absent; and (3) a cool–dry season from February to May, when the surface temperature falls to approximately 22°C and there is low rainfall.

Methods: A total of 562 individuals of *Octopus hubbsorum* were obtained from the commercial artisan catches made by local fishermen at three different localities of the central region of Jalisco. Time of capture was between 8:00 a.m. and 3:00 p.m. at depths shallower than 30 m. Collection of individuals began in July of 1999 and ended in August of 2000.

The dorsal mantle length (DML), total body weight, and sex of each individual were first determined in the field, and then all individuals stored at −20°C. After thawing, the maturity stage was assigned in the laboratory using the scale of Guerra (1975) as revised by Cortez et al. (1995).

To analyze the diet and feeding habits, a total of 226 specimens were used. The visceral mass of each specimen was separated (by dissecting the mantle) and weighed (±0.1 g). Also, the digestive tract was separated from the rest of the visceral mass and weighed (±0.01 g). The contents of the digestive tract was then separated and the prey items were counted and identified to the lowest possible taxon. The different types of prey were grouped according to taxonomic affinities, resulting in five putative groups: mollusks (including only gastropods and bivalves), cephalopods, crustaceans, teleosts (bonefishes) and other items. Several indices were used to describe the diet and to compare the items according to sex, size, stage of maturity, and the seasons of the year (Hyslop, 1980; Castro & Guerra, 1990; Sánchez and Obarti, 1993; Cortez et al., 1995):

1. Fullness Index $FI = (Wsc/Wt) * 100$

   Wsc = weight of the stomach contents. Wt = total weight of the specimen (Hyslop, 1980). The results of FI were grouped in levels according to the different degrees of filling of the stomachs, as suggested by Hernández-López (2000): $FI = 0$ (level I, empty stomach); $0 < FI \leq 0.3$ (level II, almost empty stomach), $0.3 < FI < 1$ (level III, half full stomach), $FI \geq 1$ (level IV, full stomach).

2. Vacuity Index $VI = (Es/Ts) * 100$

   Es = number of empty stomachs, Ts = total number of stomachs analyzed (226).

3. Occurrence Index $OI = \left(Ne_i \Big/ n \sum_{Ne}^{i=1} \right) * 100$

   Ne_i = number of stomachs with the prey item i; $n \sum_{Ne}^{i=1}$ = total number of different prey species.

4. Importance in Weight Index $IWI = (Wi/Wt) * 100$

   Wi = weight of each type of prey i, Wt = total weight of all prey items.

5. Importance in Number Index $INI = (Ni/Nt) * 100$

   Ni = number of individuals of each type of prey i, Nt = total number of individuals of all prey items.

To analyze the influence of size on the diet and the feeding habits of *O. hubbsorum*, two groups were considered: (1) juveniles (60–100 mm DML) and (2) adults (>100 mm DML). Among the adults, three maturity groups were compared: immature, mature, and senescent (females) or discharged (males). Maturing specimens were included in the mature group. The seasons of the year considered for these analyses were (1) warm–wet season (June to September), (2) warm–dry season (October to January) and (3) cool–dry season (February to May).

Comparisons of the indices (*FI*, *VI*, *OI*, *IWI*, and *INI*) between groups were made by means of a chi-square test (Sokal & Rolf, 1969). The level of statistical significance used was $\alpha = 0.05$.

RESULTS

Size and sex proportion of the octopus population: Figure 2 shows the size (dorsal mantle length, DML) and stage of maturity (immature, mature, and senescent) of 514 individuals of *Octopus hubbsorum* sampled from the commercial artisan catches in the central region of Jalisco. The DML ranged from 43 to 230 mm (mean = 110.43 mm ± SD 42.78 mm). The sex proportion was 1.35:1 (296 females, 218 males). The larger sizes (DML) were recorded for the females (t = 3.29; $P < 0.01$), range 43 to 230 mm (mean = 111.36 ± SD 26.33 mm) and the smaller sizes for the males, range 43 to 162 mm (mean = 104.49 ± SD 21.49 mm).

Composition and conservation of the prey items: A total of 53 different prey items were identified in the stomach content of the octopuses. These items included almost

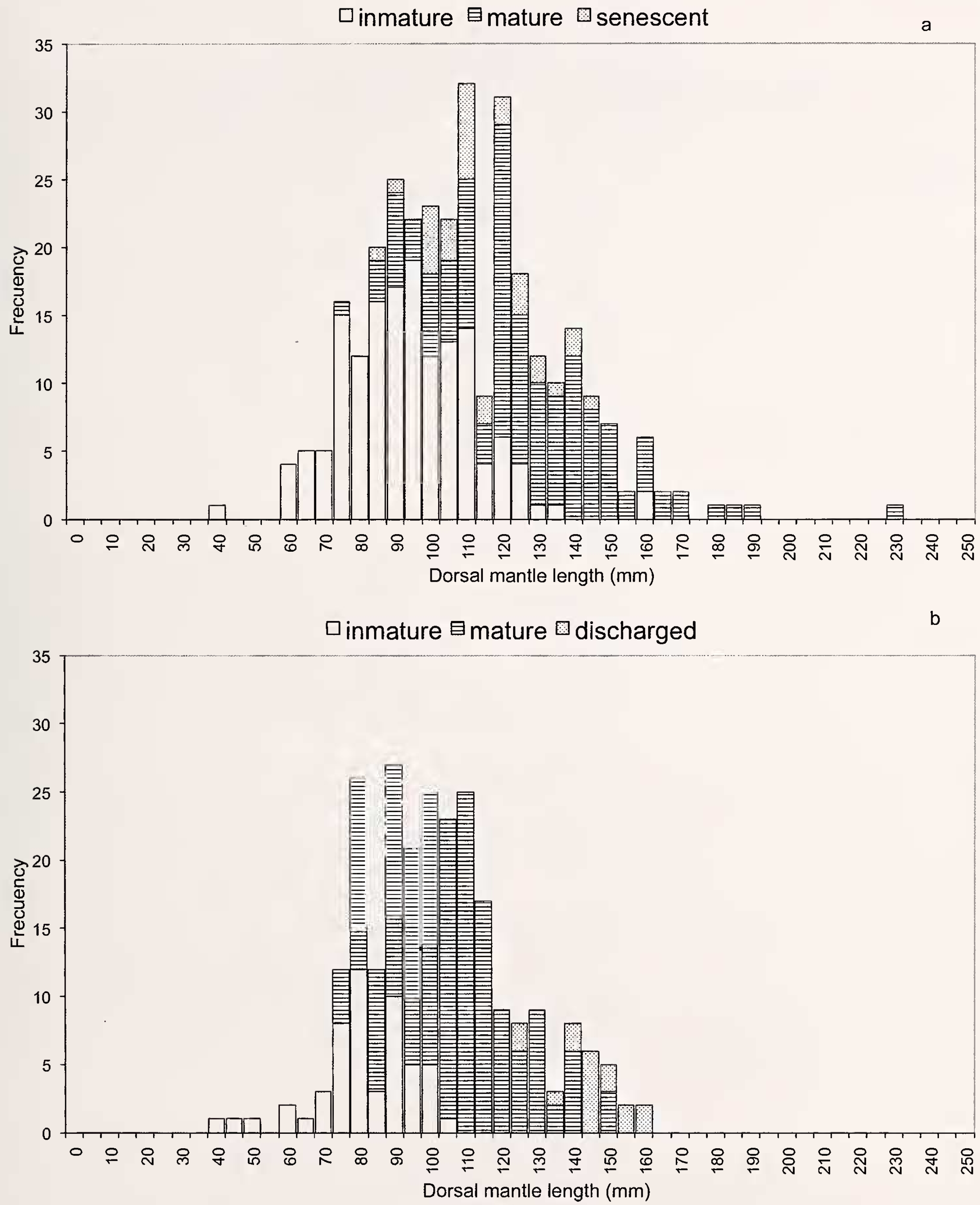
inmature
mature
senescent
a
Frecuency
Dorsal mantle length (mm)
inmature
mature
discharged
b
Frecuency
Dorsal mantle length (mm)

Figure 2.

Table 1

Composition of diet of *Octopus hubbsorum*.

			Ocurrence (*N*)		Weight (g)		Number (*N*)	
			total	%	total	%	total	%
Crustacea			294	57	225	46	2157	88
Estomatopoda			16	3%			22	1%
	Gonodactylidae	*Neogonadoctylus stanchi*						
	Pseudosquillidae	*Pseudosquilla adiastalta*						
Caridea			77	15%			192	8%
	Palaemonidae	*Pontonia* sp.						
	Alpheidae	*Alpheus malleator*						
		Alpheus lottini						
		Alpheus sp.1						
		Synalpheus digueti						
		Synalpheus nobilii						
		Synalpheus sp.						
Anomura			14	3%			20	1%
	Porcellanidae	*Clastotoechus diffractus*						
		Pachycheles biocellatus						
		Pachycheles panamensis						
		Pachycheles sp. 1						
		Pachycheles sp. 2						
		Petrolisthes edwardsii						
		Petrolisthes glasselli						
		Petrolisthes haigae						
		Petrolisthes sp. 1						
		Petrolisthes sp. 2						
Brachyura			187	36%			1923	79%
	Majidae	*Mithrax denticulatus*						
		Mithrax sp.						
		Thoe sulcata sulcata						
		Teleophrys cristulipes						
	Xanthidae	*Paractaea sulcata*						
		Microcassiope xantusii						
		Xanthodius stimpsoni						
		Liomera cintimana						
		Platyactaea dovii						
		Pilumnus gonzalensis						
		Paraxanthias insculptus						
Mollusca			152	30%	124	26%	199	8%
Cephalopoda			54	11%	86	18%	72	3%
	Octopodidae	*Octopus hubbsorum*						
		Octopus sp.						
			98	19%	38	8%	127	5%
Bivalvia			27	5%	7	1%	36	1%
	Mytillidae	*Modiolus* sp.						
		Unidentified No. 1						
	Unidentified No. 1							
	Unidentified No. 2							
	Unidentified No. 3							
Gastropoda			71	14%	31	6%	91	4%
	Muricidae	Unidentified No. 1						
		Unidentified No. 2						
	Unidentified No. 1							
	Unidentified No. 2							
Pisces			41	8%	116	24%	47	2%
Teleostei			41	8%	116	24%	47	2%
	Muraenidae							
	Unidentified No. 1							
	Unidentified No. 2							

Table 1

Continued.

			Ocurrence (*N*)		Weight (g)		Number (*N*)	
			total	%	total	%	total	%
Others			27	5%	19	4%	42	2%
Annelida	Polychaeta	Unidentified No. 1						
		Unidentified No. 2						
Chaetognatha								
	Aphragmopohora	Unidentified No. 1						
Echinodermata								
	Diadimastidae	Unidentified No. 1						
		Unidentified No. 2						
	Equinometridae	Unidentified No. 1						
		Unidentified No. 2						
	Ophiuroidea	Ophiocomidae sp.						
Talophytas		*Padina* sp.						
Total			514	100%	485	100%	2445	100%

complete prey and fragments of several body structures in different stages of digestion. Only a small percentage (5%) was recorded as consisting of complete and freshly eaten organisms, while almost 95% of the material was fragmented or partially digested. Organisms from seven taxonomic groups were identified (Table 1): Thallophytes (macroalgae), Annelida, Arthropoda (subphylum Crustacea), Mollusca, Echinodermata, Chaetognata, and Chordata (subdivision Teleostei).

The taxonomic identification of crustaceans was based on the carapaces, rostra, dactyls, chelipeds, other appendages, and eggs in different stages of maturity. In the case of gastropod mollusks, the identification was made using the opercula and fragments of shells; in the case of bivalve mollusks, using fragments of the valves and the byssus. The octopod prey were recognized using body fragments (arms, beaks, and lenses) or the almost complete small juveniles; the egg masses of other octopuses were also present in the stomachs. Complete chaetognath individuals were found in the samples, but only fragments of spines and body fragments of echinoderms, including their characteristic mouthparts. The polychaetes were identified using body fragments with multiple appendages. Recently caught fishes were almost complete, and other body parts (spines, bones, scales, and otoliths) were also present. Finally, the small pieces of macroalgae in the samples are probably an indication of the habitat or substratum where the prey were caught by the octopuses.

Diet: The diet of *O. hubbsorum* is composed mainly of members of three groups: mollusks, crustaceans, and fishes. The crustaceans dominated in the samples, according to the frequency of their occurrence in the samples (57%), their weight (46%), and their number (88%). The brachyuran decapods occurred in 36% of the samples and represented 79% of the total number of prey. Other decapod crustaceans, the carideans, and anomurans, were less common in the samples (15% and 3%, respectively). The mollusks were the second most important group according to the frequency of their occurrence in the samples (30%), their weight (26%), and their number (8%). Cannibalism of *O. hubbsorum* was important in frequency (11%) and weight (18%),

Table 2

Values of the Fullness Index (FI) for the females, males, and total individuals of *Octopus hubbsorum*. Content in the digestive tract: I (empty), II (almost empty), III (half full), IV (full).

	Females				Males				Total			
	I	II	III	IV	I	II	III	IV	I	II	III	IV
Juvenile	14.81	53.70	31.48	0	11.53	53.84	34.61	0	13.20	53.77	33.01	0
Adult	29.69	38.46	27.69	4.61	10.63	70.21	19.14	0	21.42	51.78	24.10	2.67

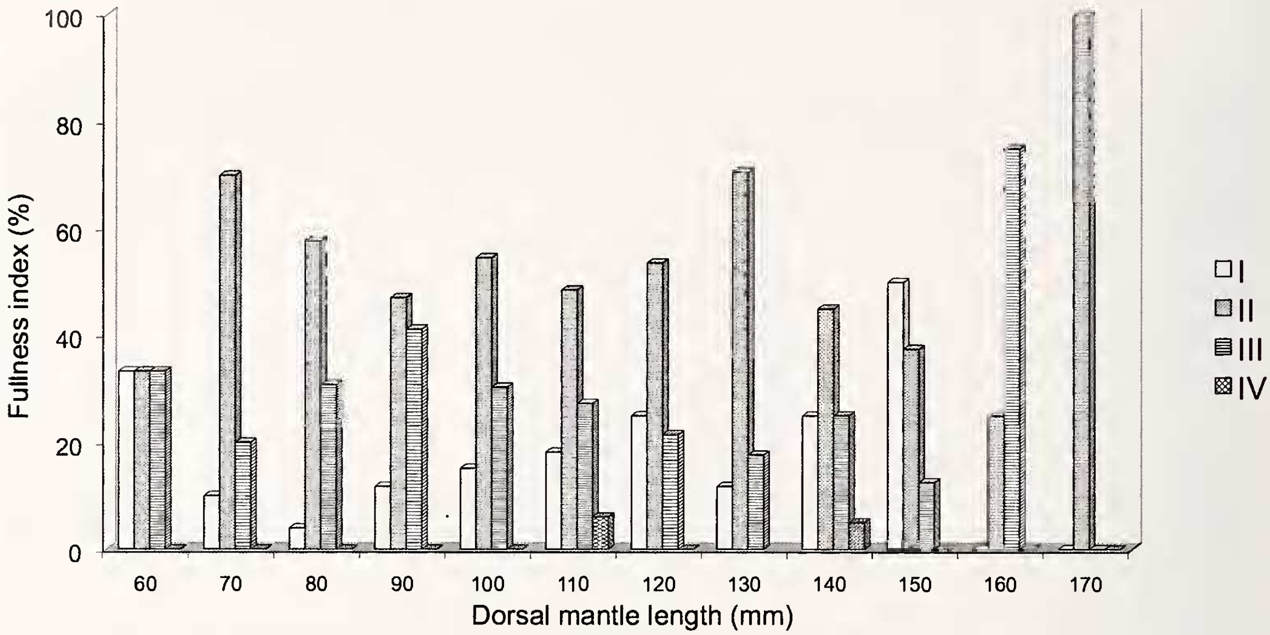

Figure 3.

but it represented only 3% in number. Teleost fishes were the third most important taxonomic group, according to their occurrence in the samples (8%), weight (24%), and number (2%); the presence of juvenile moray eels (family Muraenidae) is probably unusual for *O. hubbsorum*. Finally, the prey items belonging to the phyla Talophyta, Annelida, Echinodermata, and Chaetognata showed percentages lower than 5% in occurrence, weight, and number, and they were combined in the group "others." Most prey items of this group were not identified to species, and some were probably incidental, as in the case of the macroalgae.

Fullness index (*FI*): The results indicate that *O. hubbsorum* feeds almost constantly in the area of study. Most octopuses analyzed (126 females and 100 males) contained prey in their digestive tracts with different degrees of fullness. According to the Fullness Index (*FI*), nearly 80% of the stomachs were in the categories II (almost empty) or IV (full) (Table 2; Figure 3). The amount of food in the stomachs was significantly different among females and males ($X^2 = 4.73$; df = 1; $P < 0.05$); the females recorded higher amounts than males. The total population showed a tendency to decrease the amount of food with the size of the individuals. This tendency was more evident among the females, more of which had stomachs in category II (almost empty). Category IV (full) was observed only in the stomachs of adult females. Although the values of *FI* were higher during the warm–dry season, there were no significant differences between the seasons of the year ($P > 0.05$). Females showed higher *FI* values (>26%) than males during the period of study ($X^2 = 8.72$; df = 3; $P < 0.03$), except during the warm–dry season ($P > 0.05$) (Table 3).

Vacuity index (*VI*): Nearly 20% of the stomachs of *O. hubbsorum* were empty. There were no significant differences in the Vacuity Index (*VI*) between females

Table 3

Seasonal values of the Fullness Index (FI) for the females, males, and total individuals of *Octopus hubbsorum*. Content in the digestive tract: I (empty), II (almost empty), III (half full), IV (full).

	Females				Males				Total			
	I	II	III	IV	I	II	III	IV	I	II	III	IV
Warm–wet	24.48	44.89	28.57	2.04	20	70	10	0	23.18	52.17	23.19	1.45
Warm–dry	7.69	53.84	38.46	0	12.5	45.83	41.66	0	10	50	40	0
Cool–dry	26.66	42.22	26.66	4.44	7.69	67.30	25	0	16.66	55.21	26.04	2.08

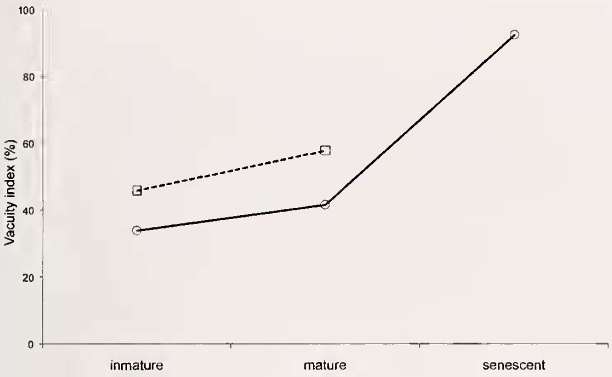

Figure 4.

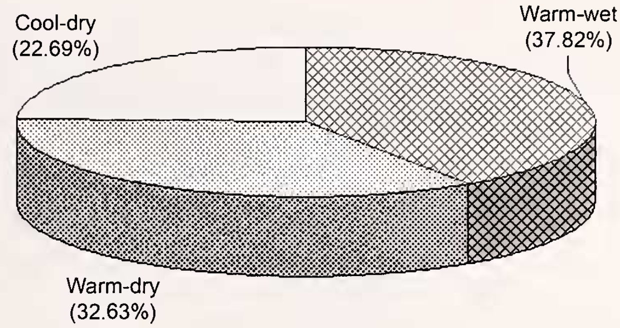

Figure 5.

and males ($P > 0.05$). Figure 4 shows the tendency of the *VI* vary according to the maturity stage. There was no significant difference in the *VI* between immature and mature individuals ($P > 0.05$). However, the proportion of empty stomachs increased to nearly 85% in the senescent females, and the value of the index was significantly different ($X^2 = 16.39$, $P < 0.001$). The values of the males and females were not significantly different in immature ($P = 0.169$) and mature ($P = 0.056$) individuals. On the other hand, there were significant differences in the proportion of empty stomachs observed between the seasons of the year. The warm–wet season showed the highest proportion of empty stomachs (37.82%), while the lowest was observed in the cool–dry season ($X^2 = 6.55$, $P = 0.038$) (Figure 5).

Occurrence index (*OI*), importance in weight index (*IWI*), and importance in number index (*INI*): The relative importance of each group of prey (crustaceans, mollusks, fishes, cephalopods, and "others") depended of the index in which it was expressed: *OI*, *IWI* or *INI*. The Kruskal-Wallis test indicated differences between juveniles (60–110 mm DML) and adults (>110 mm DML) in the indices of occurrence (*OI*) (H = 41.61; $P < 0.005$), weight (*IWI*) (H = 31.96; $P < 0.001$), and number of prey (*INI*) (H = 20.17; $P < 0.028$). The values of the three indices increased between the interval of 65 mm and 110 mm DML (Figure 6, 7, and 8), and decreased gradually toward the larger sizes.

The *IWI* values showed differences in the feeding habits between males and females of *Octopus hubbsorum*. The crustaceans and the group "others" were preferred by males, while the females preferred the mollusks (gastropods and bivalves) and fishes (Table 4). In the cases of cannibalism (cephalopod prey), there was no clear pattern of preference between sexes.

The variety and proportion of new prey items in the diet increased with the size of the individuals. This was more evident in the case of crustacean prey, which declined in importance in the stomach contents as the size of the octopuses increased from 75 mm to 160 mm DML. Consequently, the importance of other prey (gastropods, bivalves, cephalopods, fishes, and "others") increased in these individuals, suggesting a change in the feeding habits with increasing size. This pattern was also observed in the *IWI* and *INI* (Figures 7 and 8). The Kruskal-Wallis tests indicate significant differences in the values of *IWI* and *INI* between the size intervals ($H = 41.74$, $P < 0.001$; $H = 20.17$, $P < 0.028$, respectively).

Dietary comparisons of the different groups of prey as a function of the size revealed that the mollusk prey were more important in juvenile individuals (<110 mm DML), while the cephalopod prey were more important in the adults (>110 mm DML) of both sexes (Table 4). The fishes were more important in the juvenile females and in the adult males. No differences were found in the crustaceans and the group "others" between juveniles and adults.

The *IWI* showed higher values in the inmature individuals of both sexes for crustaceans and the group "others" (Table 5); similar results were found in juveniles and adults (Table 4). The mollusks, cephalopods, and fishes were more important in the mature and senescent octopuses (Table 4b). The *INI* values showed significant differences between sexes only in the group "others": the males had more prey items from this group (Table 6).

All groups of prey had variations in the values of *OI*, *IWI*, and *INI* during the period of study (Figure 9). The males showed a more evident pattern; the three indices had a tendency to increase from the warm–wet season to the cool–dry season. The cool–dry season not only showed the highest values of *OI*, *IWI*, and *INI*, but also the highest proportion of cephalopods and teleost fishes. The crustaceans were dominant at all times, with values above 40% in both sexes. However, crustaceans increased their occurrence (*IO*) and weight (*IIW*) in the samples during the warm–wet season ($P < 0.05$), but not their impor-

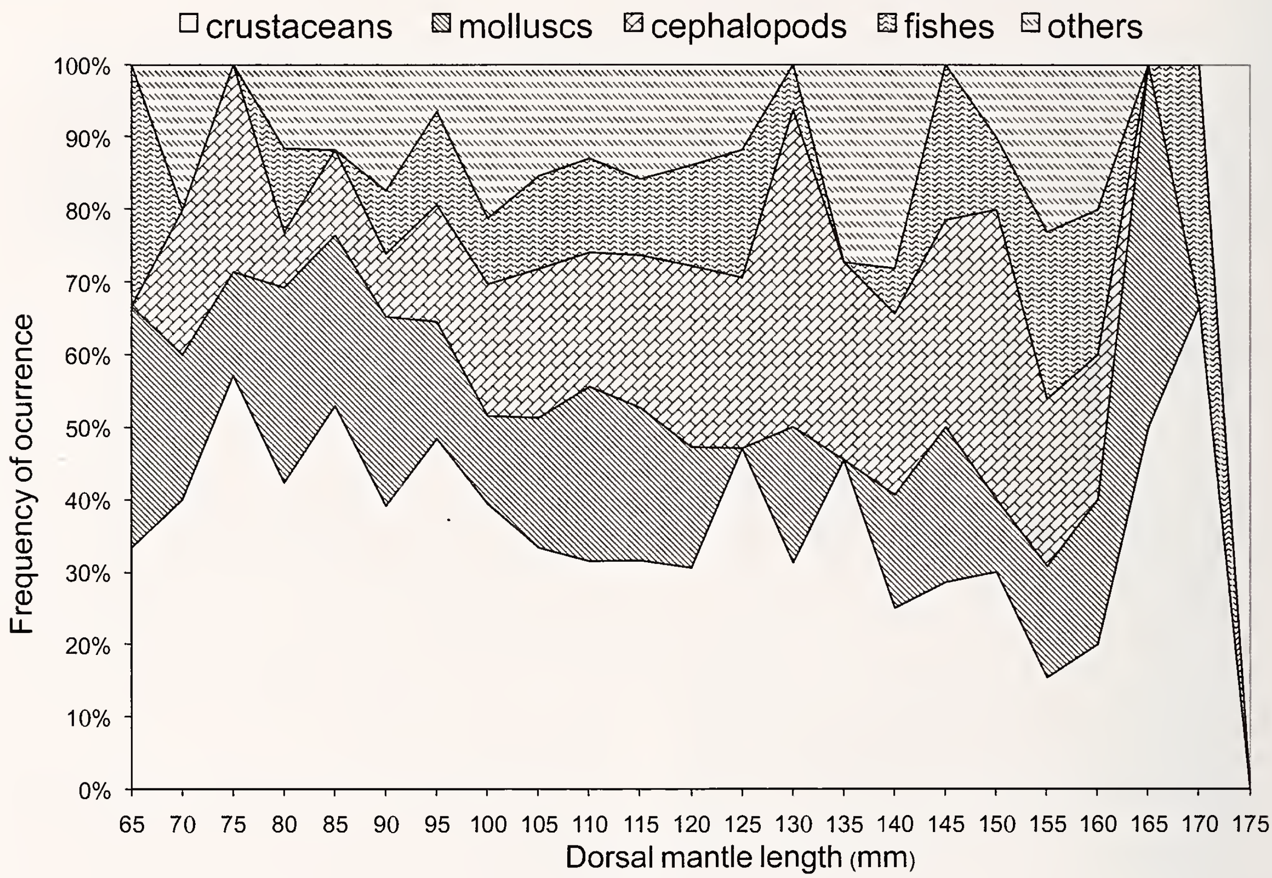

Figure 6.

tance in number (*IIN*). The high proportion of crustaceans in the digestive tracts during the warm–wet season is remarkable, with percentages between 81% and 97% for the three indexes. During the warm–dry season, the mollusks were significantly more important in the samples according to the *OI* and *IWI* values ($P < 0.05$), but not according to the *INI* value.

According to the *OI* and the *IWI*, the females and males followed a similar pattern, since the participation of the five groups of prey increased from the warm–wet season to the temperate–dry season. However, this tendency was not clear with the *INI*. The participation of crustaceans was always important, with values between 40% and 90% of the *INI*. In general, mollusks (gastropods, bivalves, and cephalopods) were best represented during the warm period of the year (warm–wet and warm–dry seasons).

DISCUSSION AND CONCLUSIONS

Previous studies on the diet of other species of *Octopus* report that they are active carnivores that feed mainly on crustaceans, mollusks, and fishes, while echinoderms, polychaetes, chaetognaths, and siphonophores form part of their diet in smaller proportions (Nixon, 1987; Guerra, 1978; Smale and Buchan, 1981; Ambrose, 1984; Cortez et al., 1995; Grubert et al., 1999). Additionally, these studies describe significant changes in the relative importance of the prey as a function of the sex, size, stage of maturity, and the season of the year. The diet and feeding habits of *O. hubbsorum* in the central Mexican Pacific is consistent with these descriptions.

The method employed for assessing the diet is very important, since some procedures may overemphasize the importance of some kinds of prey relative to others. For example, the use of traps to asses the diet of *O. vulgaris* may result in a higher proportion of fishes relative to other prey, especially invertebrates, because octopuses and fishes were caught together in the traps (Hernández-Lopez, 2000). Also, a procedure based on the collection of food debris around octopus middens would not record the consumption of fishes (Ambrose & Nelson, 1983; Ambrose, 1986; Mather, 1991). The only previous record on the diet of *O.*

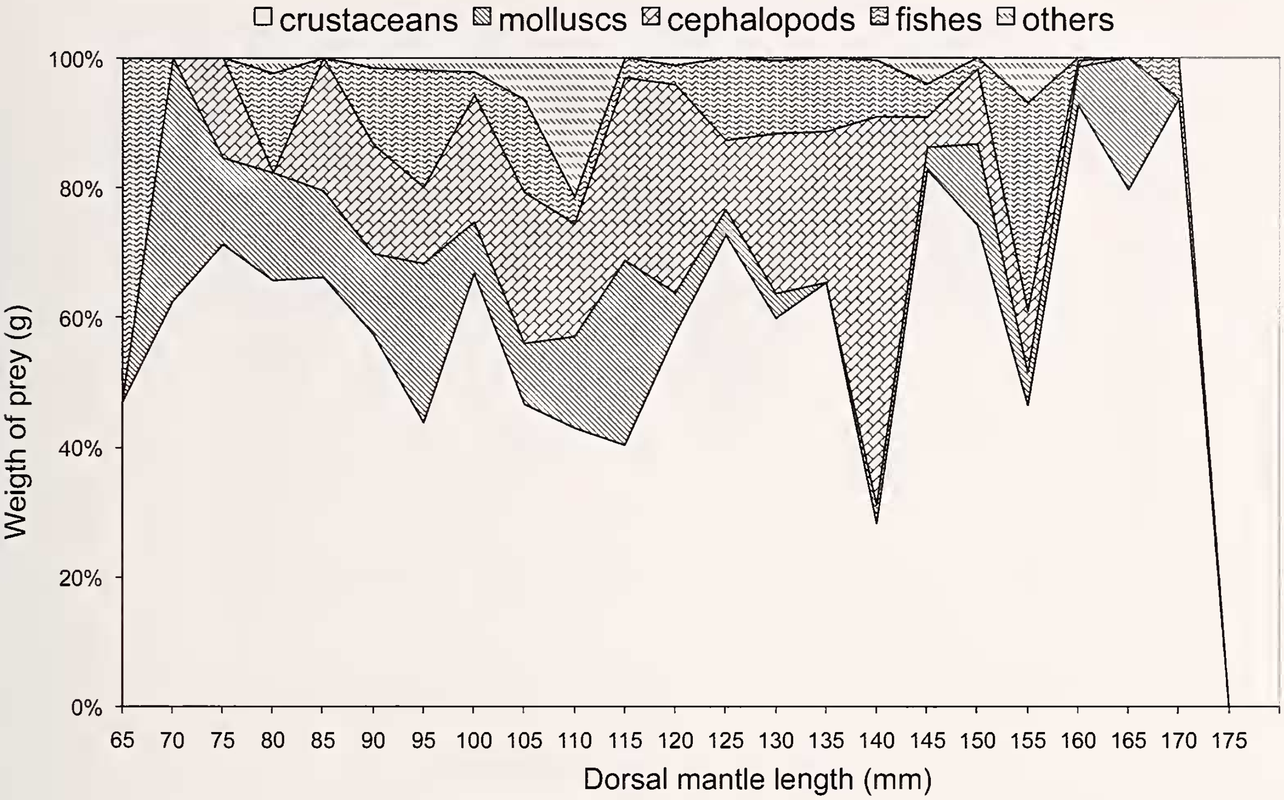

Figure 7.

hubbsorum was based on this latter procedure (Raymundo, 1995), which indicated only remains of crustaceans and shells of gastropods and bivalves. The study of the content of the digestive tracts has been commonly used to study the diet of *Octopus* spp., and it is considered a reliable method because it gives evidence of the consumption of invertebrates and fishes with hard skeletons and shells that may be used for taxonomic identifications.

A good evaluation of the diet of cephalopods should take into consideration a sample size that represents the different members of the natural populations, including juveniles, adults, and the senescent of both sexes. The sample size may be different according to the cephalopod species. Shchetinnikov (1986) estimated that approximately 20 stomachs per sample were enough to describe the diet of squid populations from the oceanic waters off Peru. Grubert et al. (1999) used a sample of 137 male and female individuals to describe the diet and feeding strategy of *Octopus moarum* along the southeastern coast of Tasmania. In the Canary Islands, Hernández-López (2000) determined experimentally that a minimum sample size of 13 stomachs per month of *Octopus vulgaris* was sufficient to obtain 80% of the prey categories for this species. In the present study, a sample of 226 individuals of *O. hubbsorum* of both sexes from a wide range of sizes and different stages of maturity were analyzed during an annual cycle. The general coincidence in the feeding habits of *O. hubbsorum* with other species of *Octopus* and the ample variety of prey items found suggests that the methodology and the sample size were satisfactory.

It is known that octopods are active hunters at night; they search for food mainly during the sunrise and sunset hours and make only short infrequent feeding trips during the day (Mather & O'Dor, 1991; Mather, 1991). The time of the day may also affect their feeding habits; for example, predation of *O. vulgaris* on fishes may change during the diurnal and nocturnal periods of the day (Nigmatullin & Ostapenko, 1976). Most octopods digest rapidly; in some species, the digestive process may last 14 hr at temperate temperatures (Boucher-Rodoni et al., 1987); in the case of *O. cyanea*, individuals required 12 hr to complete the digestion at 30°C (Boucher-Rodoni, 1973). Our observations suggest that *Octopus hubbsorum* has nocturnal feeding behavior because most individuals were caught during the morning

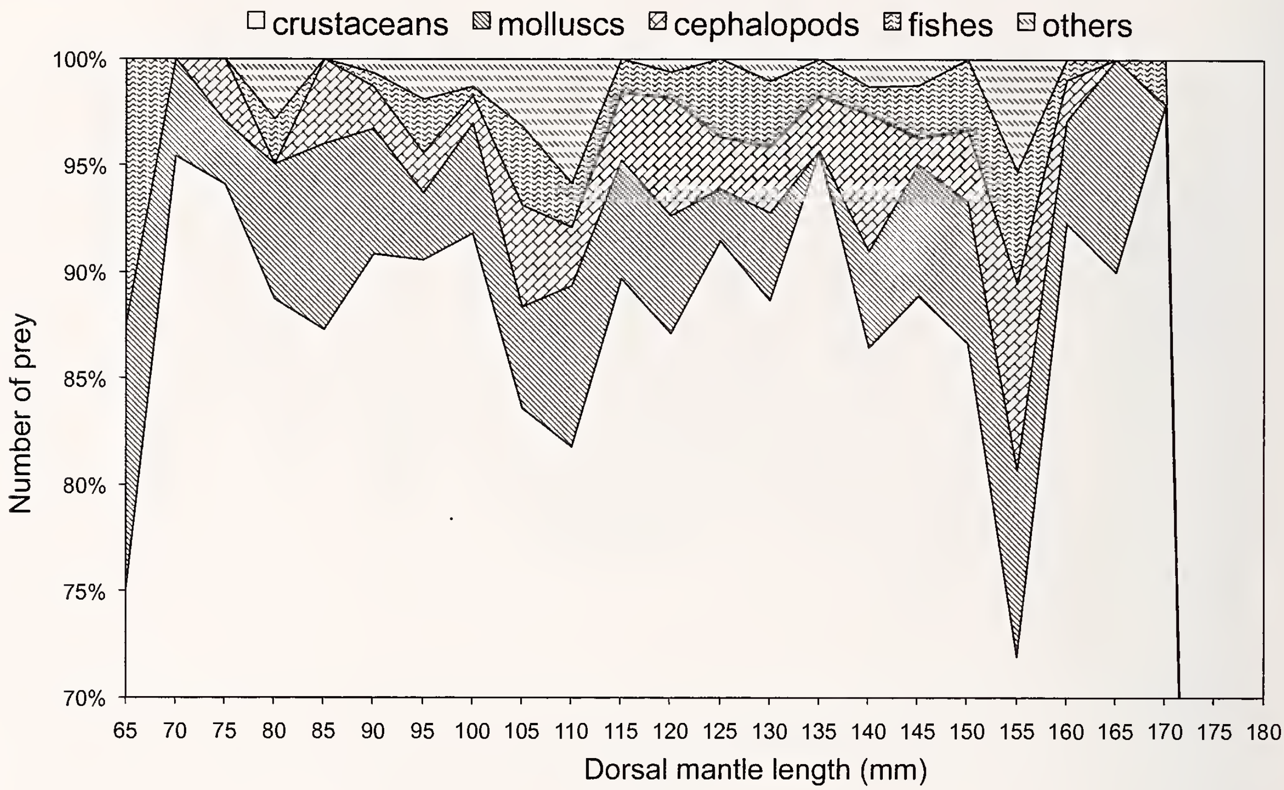

Figure 8.

hours with food in their stomachs, indicating that the prey had likely been eaten recently or only a few hours before. However, since all individuals were obtained from commercial catches during a short time span (between 8:00 a.m. and 3:00 p.m.), there is no evidence of possible variations in the predatory behavior as a function of the time of the day. Future research should extend sampling to other periods of the day to obtain a better knowledge on the natural diet and the feeding habits of this species in the central Mexican Pacific.

Octopus hubbsorum feeds on nearly 50 different prey species during the year. This is a relatively broad diet, compared with other species of *Octopus*; for example, 22 and 28 species were found in *O. vulgaris* (Ambrose & Nelson, 1983; Mather, 1991), 25 species were found in *O. dofleini* (Hartwick et al., 1981), and 12 species were found in *O. maorum* (Grubert et al., 1999). However, the dietary ranges of those other species are likely to be greater, since all of those studies were performed in relatively limited time spans (18 days to 8 months). The diversity of prey items found in *O. hubbsorum* is comparable with the 55 prey species found in a four-year study of *O. bimaculatus* (Ambrose, 1984), which was considered the practical limit of prey for that species.

Similar groups of prey have been reported in natural populations of other species of *Octopus*, such as *O. vulgaris* (Nigmatullin & Ostapenko, 1976; Guerra, 1978; Hatanaka, 1979; Smale & Buchan, 1981; Sánchez & Obarti, 1993; Hernández-Lopez, 2000), O. *bimaculatus* (Ambrose, 1984), *O. mimus* (Cortez et al., 1995) and *O. maorum* (Grubert et al., 1999). All of those species feed mainly on crustaceans, mollusks, and teleost fishes, although their relative importance in the diet varies as a function of the species.

Since cephalopods are opportunistic predators, they should consume different prey according to their availability. Therefore, the area in which the species live should affect their diet (Nixon, 1987; Hartwick et al., 1981; Ambrose, 1984). Thus, the same species may have differences in the types of prey consumed as a function of the distribution of the populations. This is evident in the case of the populations of *O. vulgaris* from the North Atlantic coast of Africa (Guerra, 1978) and the Mediterranean Sea (Sánchez & Obarti, 1993). The variety and availability of the prey is, in turn, generally related to the complexity of the habitat.

Octopus hubbsorum is the target species in the octopus fisheries of the Mexican Pacific (Aguilar-Chávez, 1995; Ríos-Jara et al., 2001). The fishermen

Table 4

Comparisons of the Importance in Weight Index (IWI) between sexes and size of the individuals of *Octopus hubbsorum*. * = significant, ** = highly significant.

Prey	Total			Juveniles			Adults			Females			Males		
	♀		♂	♀		♂	♀		♂	Juvenile		Adult	Juvenile		Adult
Crustacea	55.81	**	62.68	57.57	*	65.41	54.54	*	61.10	57.57	ns	54.54	65.40	ns	61.10
Mollusca	18.19	**	8.78	21.21	**	13.32	16.62	**	5.89	21.21	*	16.62	13.32	**	5.89
Cephalopoda	15.53	ns	13.47	6.66	*	10.93	21.02	*	15.09	6.66	**	21.02	10.93	*	15.09
Teleostei	9.43	*	6.66	13.48	**	2.78	6.79	**	9.08	13.48	**	6.79	2.78	**	9.08
Other	1.01	**	8.40	1.06	**	7.55	1.01	**	8.83	1.06	ns	1.01	7.55	ns	8.83
Total 100 %	1749		1318	660		503	1089		815	660		1089	503		815
χ^2 (g.l. = 4)		161.4			86.9			125.6			79.4			43.6	
p:		<0.001			<0.001			<0.001			<0.001			<0.001	

Table 5

Comparisons of the Importance in Weight Index (IWI) between sexes and stage of maturity of the individuals of *Octopus hubbsorum*. * = significant, ** = highly significant.

Prey	Immature			Mature			Females					Males		
	♀		♂	♀		♂	Immature		Mature		Senescent	Immature		Mature
Crustacea	58.52	**	68.79	51.13	*	56.80	58.52	**	51.13	**	41.02	68.79	**	56.80
Mollusca	19.01	**	6.03	12.78	ns	11.25	19.00	**	12.78	**	36.41	6.03	**	11.25
Cephalopoda	9.33	*	13.27	28.54	**	13.88	9.33	**	28.54	**	10.76	13.27	ns	13.88
Teleostei	12.32	**	0.51	7.00	**	11.94	12.32	**	7.00	ns	7.17	0.51	**	11.94
Other	0.80	**	2.72	0.52	**	6.11	0.80	ns	0.52	**	4.61	11.38	**	6.11
Total 100%	898		580	598		720	868		571		195	580		720
χ^2 (g.l. = 4)		194.1			71.3			96.3		80.8			89.11	
p:		<0.001			<0.001			<0.001		<0.001			<0.001	

Table 6

Comparisons of the Importance in Number Index (INI) between sexes and stage of maturity of the individuals of *Octopus hubbsorum*. * = significant, ** = highly significant.

Prey	Total ♀		♂	Adults ♀		♂	Immatures ♀		♂	Females Immature		Mature		Senescent	Males Immature		Mature
Crustacea	87.55	ns	88.72	87.15	ns	88.91	89.16	ns	91.06	89.16	ns	88.11	**	64.15	91.06	*	86.44
Mollusca	5.82	ns	4.51	6.37	ns	4.41	5.62	*	2.98	5.62	ns	4.41	**	22.64	2.98	*	6.02
Cephalopoda	3.42	ns	2.53	3.52	ns	2.62	2.19	ns	1.86	2.19	*	4.41	ns	5.66	1.86	ns	3.20
Teleostei	2.25	ns	1.50	2.37	ns	1.54	2.19	*	0.55	2.19	ns	2.20	ns	3.77	0.55	*	2.44
Other	0.94	**	2.72	0.57	**	2.50	0.82	**	3.53	0.82	ns	0.84	ns	3.77	3.53	ns	1.88
Total 100%	1376		1088	1051		839	729		537	729		589		53	537		531
χ^2 (g.l. = 4)		16.37			18.43			22.15			6.01		35.02			17.10	
p:		<0.003			<0.001			<0.001			0.198		<0.00-1			<0.002	

capture this species from the intertidal and shallow subtidal zones to depths of 30 m during semiautonomous diving. This octopus is uncommon in the intertidal zone, and it is typically found hiding in crevices and small caves in the rocky and coralline (stony coral) substrates that are more common in the shallow areas. These substrates offer a variety of microhabitats, and they support a wide selection of potential prey species. Reports on the distribution and abundance of benthic species of mollusks and crustaceans from the coast of Jalisco indicate that the prey species of *O. hubbsorum* are common in the shallow subtidal environments in which this species lives (Yáñez-Rivera, 1989; Schmidtsdorf, 1990; López-Uriarte & Ríos-Jara, 2004; Ríos-Jara et al., 2006).

There is no information on the bathymetric distribution of *O. hubbsorum*. According to local fishermen (personal communications), there are certain periods of the year when larger individuals (adult females and males) are found more frequently than usual at shallower depths. This suggests seasonal vertical movements of the adult individuals that may be related to changes in the diet through a depth gradient. If the senescent (postspawing) females of *O. hubbsorum* behave like the senescent females of other octopus species, then they reduce their feeding activity and remain close to the eggs while brooding. Thus, they would be found more frequently, during certain periods of the year, in the crevices and caves of the shallower rocky and coralline areas where fishermen usually dive. These vertical movements could explain not only the differences in the diet of the adult individuals but also the seasonal differences in the prey composition found through the year of study.

The feeding strategy of *O. hubbsorum* is complex. The size, state of maturity, and sex of the individuals influenced their diet. The importance of the different prey species changes as the octopus grows and new species are added to the diet. The larger (>65 DML) adult and senescent individuals of *O. hubbsorum* increased the proportion of cephalopods, fishes, and the group "others" in their diet, and they reduced the consumption of crustaceans and mollusks. These individuals ingested proportionally more types of prey than the juveniles. This is a common feature of cephalopods (Boucher-Rodoni et al., 1987; Hanlon & Messenger, 1996), and it has also been documented in other species of *Octopus* (Nigmatullin & Ostapenko, 1976; Guerra, 1978; Castro & Guerra, 1990; Cortez et al.,1995).

Other reports on feeding habits of cephalopods suggest that there is not a large difference between the diet of juveniles and that of adults among the coastal species of octopuses (Boucaud-Camou & Boucher-Rodoni, 1983; Bouche-Rodoni et al., 1987).

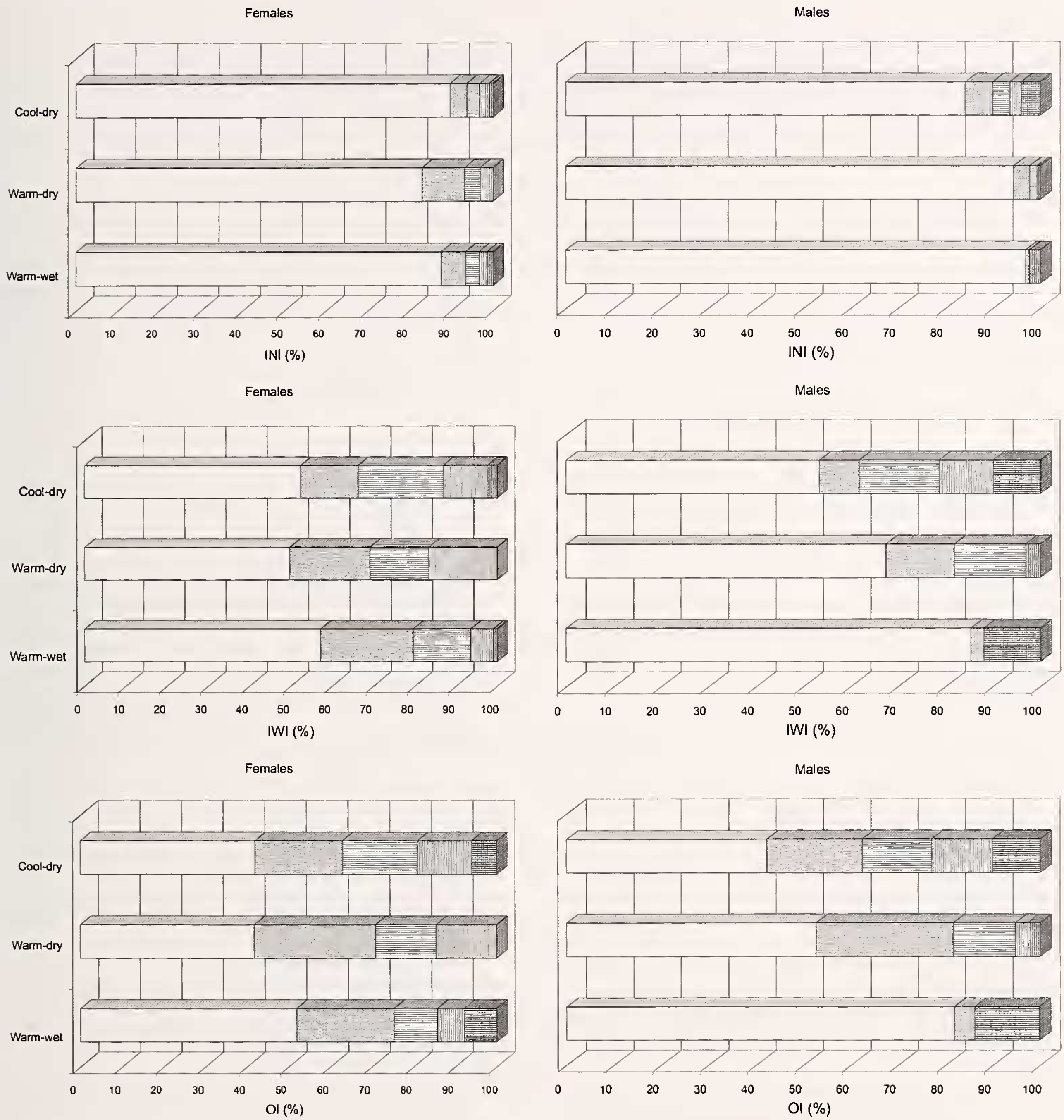

Figure 9.

Hernández-López (2000) reported some overlap in the diet among juveniles and adults of *O. vulgaris*. In the case of *O. vulgaris*, Guerra (1978) reported a change in the diet with respect to a depth gradient, particularly in the importance of the species of crustaceans consumed.

There were also significant differences in the diet between adult males and females of *O. hubbsorum*, which were probably related to the higher reproductive costs of females. A higher proportion of food by weight in adult females than in adult males of *O. minus* has been associated with differences in the nutritional needs of the two sexes (Cortez et al., 1995). Female octopuses require more energy for reproduction than males (O'Dor & Wells, 1978). In *O. vulgaris*, the high deposition of lipids in the yolk has been considered as a limiting factor for egg production by adult females (O'Dor et al., 1984). This may be true also of *O. hubbsorum* on the coast of Jalisco.

Octopus hubbsorum had a higher proportion of empty stomachs in mature and senescent females than in males of the same stages. A similar condition has been reported in other species, such as *O. mimus*, from the coast of Chile (Cortez et al., 1995); the mature females of this species have less opportunity of catching prey (Mangold, 1987). This effect has been attributed to an inhibition of the appetite due to hormonal changes during this stage in the life cycle (Wodinsky, 1978). Also, the senescent females of *O. hubbsorum* ingested proportionally more items of the group "others" than did the senescent males. Cortez et al. (1995) suggested that the increased ingestion of the group "others" among the senescent females of *O. mimus* may be related to a reduction in their feeding activity associated with their need to remain close to the eggs while brooding, so that they tend to ingest more of the food available around the octopus middens, including those small and not very motile invertebrates of the group "others."

During the annual cycle, the composition of the diet of *O. hubbsorum* did not vary very much; the crustaceans were dominant at all times, with values above 40% in both sexes. The other groups of prey had variations in their occurrence, weight, and number, depending on the sex and the season of the year. The males did not feed on cephalopods and fishes during the warm–wet season, while females did not feed on the group "others" during the warm–dry season. However, variations in the proportions of prey items were evident among the seasons of the year. This behavior is similar to that reported for *O. mimus*, in which the main prey, the fishes, decline in proportion during fall and winter as the importance of other prey, such as crustaceans, increases (Cortez et al., 1995). There is a similar change in the diet of *O. vulgaris*, in which fishes and octopods that constitute the main items of prey during winter and spring are replaced by crustaceans at the beginning of summer.

In summary, the diet and feeding habits of *O. hubbsorum* in the central Mexican Pacific are consistent with previous descriptions for other *Octopus* spp. Species-specific related behavior could be the cause of some differences, but these variations may also be related to the regional distribution of the populations studied. The results of the present study indicate that *O. hubbsorum* is an opportunistic predator that feeds during the night on a wide variety of prey. More detailed studies using different sampling methodologies at different times of the day and night are needed to allow us to learn more about the natural diet and the feeding habits of this species.

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